


# Movement-mediated community assembly and coexistence

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## ABSTRACT

Organismal movement is ubiquitous and facilitates important ecological mechanisms that drive community and meta-community composition and hence biodiversity. In most existing ecological theories and models in biodiversity research, movement is represented simplistically, ignoring the behavioural basis of movement and consequently the variation in behaviour at species and individual levels. However, as human endeavours modify climate and land use, the behavioural processes of organisms in response to these changes, including movement, become critical to understanding the resulting biodiversity loss. Here, we draw together research from different subdisciplines in ecology to understand the impact of individual-level movement processes on community-level patterns in species composition and coexistence. We join the movement ecology framework with the key concepts from metacommunity theory, community assembly and modern coexistence theory using the idea of micro–macro links, where various aspects of emergent movement behaviour scale up to local and regional patterns in species mobility and mobile-link-generated patterns in abiotic and biotic environmental conditions. These in turn influence both individual movement and, at ecological timescales, mechanisms such as

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dispersal limitation, environmental filtering, and niche partitioning. We conclude by highlighting challenges to and promising future avenues for data generation, data analysis and complementary modelling approaches and provide a brief outlook on how a new behaviour-based view on movement becomes important in understanding the responses of communities under ongoing environmental change.

**Key words:** biodiversity, animal movement, dispersal, migration, nomadism, mobile links, metacommunity, species coexistence, biotic filter, environmental filter

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## I. INTRODUCTION

Current biodiversity loss is severe and threatens human well-being (Cardinale *et al.*, 2012; Hautier *et al.*, 2015). However, predicting exactly how and where biodiversity is lost is still difficult, as the drivers are diverse and observed trends vary across scales (Tylianakis *et al.*, 2008; McGill *et al.*, 2015). To unravel trends in biodiversity, we must take a closer look at the underlying mechanisms. A strong foundation to understanding local and regional diversity and their ongoing shifts is provided by community assembly and coexistence theory (Valladares *et al.*, 2015; Bannar-Martin *et al.*, 2018). Many of the mechanisms in these frameworks that shape metacommunities and communities and maintain species coexistence are mediated by organismal movement. This is apparent for dispersal-related mechanisms such as mass effects, colonization–competition trade-offs and dispersal limitation. In these mechanisms, organismal movement promotes

diversity both directly through species' mobility patterns and indirectly through mobile-link functions of animal vectors that transport other organisms, their propagules and nutrients, or provide consumer effects (Lundberg & Moberg, 2003; Bauer & Hoyer, 2014; Gounand *et al.*, 2018). However, organismal movement can critically influence community assembly and species coexistence through many further pathways, for example, reducing exploitation competition in spatiotemporally heterogeneous environments (Macandza, Owen-Smith, & Cain III, 2012), locally strengthening predator effects on prey (Avgar, Giladi, & Nathan, 2008a), or modifying abiotic environmental filters (Shantz *et al.*, 2015).

Still, in many existing biodiversity assessments, movement is either ignored or only represented phenomenologically (e.g. by assuming certain dispersal kernels or space-use patterns). We know, however, from the field of movement ecology that movement is more complex (Nathan *et al.*, 2008a)

and requires an individual-based perspective with individuals varying in phenotypes (e.g. personality), motivation, and locally experienced environments. Ongoing extensive development of technology and analytical tools enables us to decipher how animals integrate information about their environment, experience, and innate states to make movement decisions (Kays *et al.*, 2015; Wilmers *et al.*, 2015; Hooten *et al.*, 2017). First efforts to join the process-based perspective on movement with community- and landscape-level approaches have demonstrated that individual movement capacities and strategies are critical in determining spatial population structure and within-species niche specialization (Spiegel *et al.*, 2017; Schirmer *et al.*, 2019), how prey communities form in a landscape of fear (Teckentrup *et al.*, 2018), as well as the persistence of species and communities in fragmented landscapes (Brown *et al.*, 2017; González-Varo *et al.*, 2017). Yet, a full-fledged integration of movement ecology and biodiversity research is still in its infancy (Jeltsch *et al.*, 2013; but see Barton *et al.*, 2015).

To fill this gap, we provide a comprehensive overview of the various possible pathways through which organismal movement shapes community and metacommunity composition. As this requires merging different ecological subfields and their theories and concepts, we first briefly review relevant concepts from movement ecology and community ecology. Subsequently, we synthesize movement-mediated community assembly and coexistence, focusing on mechanisms for which specific movement processes are pivotal. In this part, we highlight how an integration of a more process- and behaviour-based view of organismal movement within community ecology can help us better to understand biodiversity patterns and their ongoing changes. Next, we outline a new framework for integrating the individual-based approach of movement ecology and the population- and species-based approaches of community ecology. Finally, we describe current challenges and avenues for future research, emphasizing where we see the strongest needs and greatest potential for advancing our knowledge. We intend to stimulate research at the interface of movement ecology and biodiversity research to make better use of the impressive amount of information generated in both disciplines.

## II. BACKGROUND

Although movement ecology has emerged as a discipline relatively recently, a long tradition of observing and studying movements has generated important general insights and concepts. Likewise, community ecology has established a rich body of theory and concepts to understand patterns in community and metacommunity composition and their underlying processes. From this, we use the prominent frameworks of community assembly, modern coexistence theory, and metacommunity theory to investigate and evaluate where in these frameworks a deeper consideration of organismal movement

may bring significant gains to our understanding. In the following, we briefly summarize the core concepts from these theories that we use herein. We also include the mobile link concept (Lundberg & Moberg, 2003), which systemizes the effects of actively moving animals on ecosystem functions and more generally emphasizes their role in connecting habitats in both space and time, a feature relevant for various aspects of community-level processes.

### (1) Movement processes

Although movement can be defined rather simply as the process by which organisms change their location in time, it is a process with many facets. It has biomechanical aspects, including the proximate physiological and physical processes that put an organism's stimulus to move into effect and define its locomotion. It requires a cognitive architecture, in which an organism integrates its motivation to move, information about the environment through perception or memory, and its navigational abilities to set and reach a destination. Movement further has an optimality aspect in the sense that it may ultimately impact fitness components such as survival or reproduction, which we expect to be reflected in actual movement decisions. To deal with this broad spectrum of elements of a movement process, Nathan *et al.* (2008a) introduced the movement ecology framework, which serves as a prism in breaking down movement into three basic components – internal state ('why move?'), motion capacity ('how to move?'), and navigation capacity ('where to move?') – that in relation to the environment shape the movement path of an individual or organismal unit (see upper panel of Fig. 1). Despite, or rather because of its simplicity, this framework provides a fundamental conceptual basis to understanding organismal movement.

Among organisms there is a great variety in short-term movement goals as well as taxon-, species-, and individual-specific strategies in how, where and when to move to accomplish these goals. However, based on broad differences in the reasons (which may be evolutionary) for moving and the resulting spatio-temporal movement patterns that emerge from many movement bouts over long timescales (up to lifetimes), typically four basic movement types are distinguished: dispersal, migration, station-keeping movement (or range residency), and nomadism (see Fig. 2 for details). Within types, movement is usually further composed of bouts of varying movement modes according to different behavioural states, such as foraging movements, exploratory movements (searching), or escape movements in actively moving animals. While the characteristics of movement at this level can have implications at the community level (e.g. see Section III.3a), we use the four broad movement types to structure our review of movement-mediated community assembly and coexistence because they have possible community implications at different spatial and temporal scales. Note that we define spatial scales not in spatial units *per se*, as these vary greatly, but from the perspective of the moving individual.

While station-keeping movements are local and within a population, dispersal movements are regional and connect populations at the metacommunity scale. Occasionally, dispersing organisms may move or be transported long distances even across regions. Migratory movements are typically interregional, crossing geographic regions (e.g. migrating ungulates), ecosystems (e.g. fish migrating between fresh water and the ocean), or even continents (e.g. many migratory birds), thus providing potential links at these scales. From a population perspective, migratory animals often migrate aligned with their population and thus migration does not necessarily imply large-scale mixing within a species. However, they encounter and interact with different (meta-)communities at their breeding *versus* non-breeding sites. Therefore, also from a metacommunity perspective, migration can be considered interregional. Nomadic animals often stay within a region (e.g. bats, or birds during the non-breeding season) but may also move similar distances as migrants (e.g. nomadic gazelles), thus having the potential to link (meta-)communities.

The movement types also operate on different timescales and thereby influence communities in fundamentally different ways (Amarasekare, 2008). Many movements, such as foraging movements during station-keeping but also transition movements of migratory or nomadic animals, occur on shorter timescales than population dynamics (Fahse, 1998). Therefore, these movement processes influence community composition mainly through the emergence of certain mobility patterns that arise from a combination of multiple movement characteristics, and which impact fitness or competitive relationships among species and ultimately (meta-)community composition, as we will demonstrate herein (see also Table 1). By contrast, dispersal impacts population dynamics more directly (*via* emigration and immigration rates) resulting in more immediate effects at the community level. However, individual dispersal events are still dependent on (behavioural) movement processes on short timescales during which an organism must draw on its movement capacities and, if moving actively, make movement decisions. Thus, when considering the implications of movement processes on community and metacommunity composition, we face the challenge of having to integrate timescales.

## (2) Mobile links

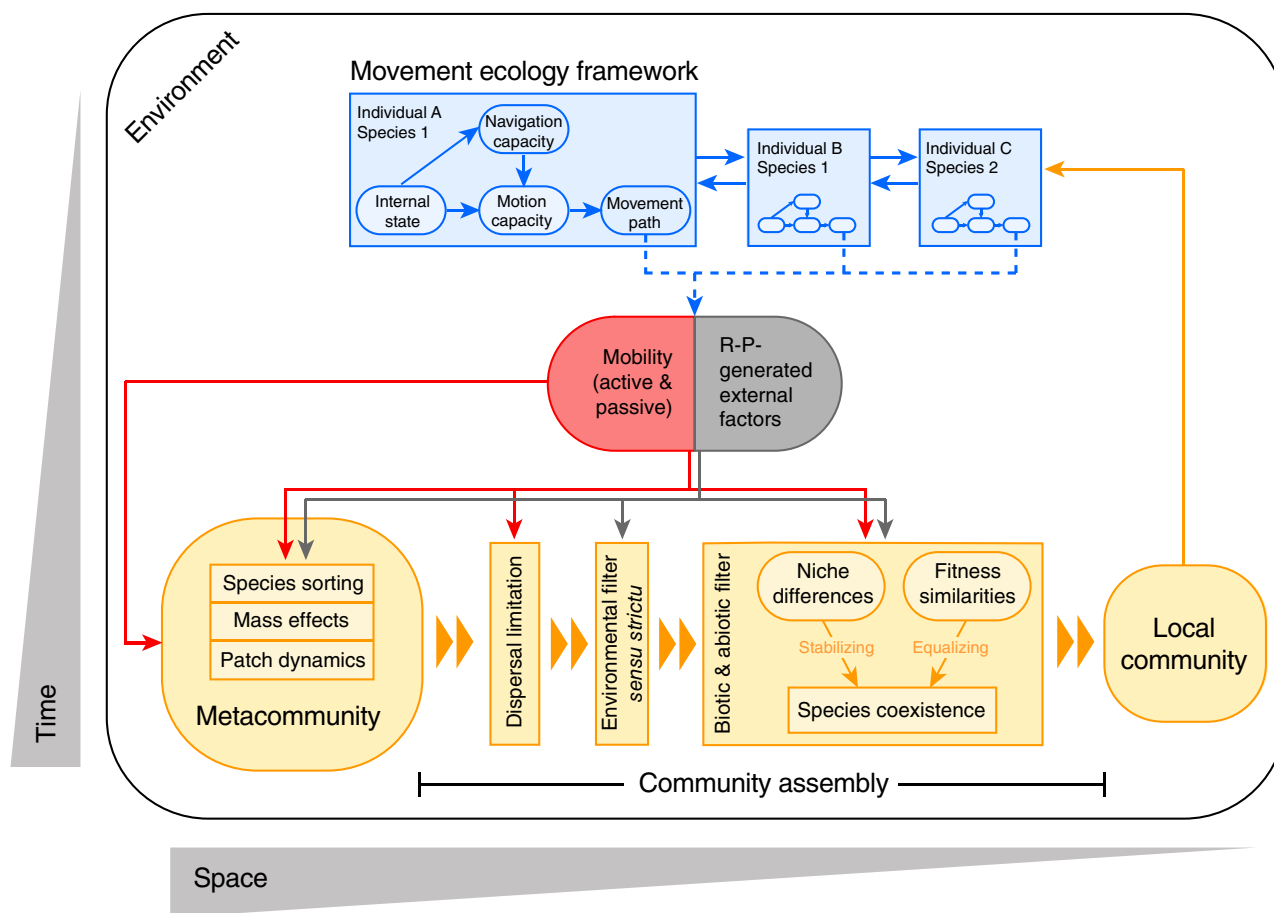
Mobile animals may not only move themselves between sites and communities, but also confer mobility to other organisms or non-living material, or create spatiotemporal patterns in processes that affect the abiotic environment or the trophic web. Whenever animals act in this way, they are considered mobile links or mobile linkers (Lundberg & Moberg, 2003). Based on what they transport, three types of mobile linkers are distinguished. Genetic linkers transport organisms (e.g. zooplankton or soil fauna) or their propagules (e.g. eggs, seeds, spores), which may attach externally (e.g. in fur or feathers) or be ingested and later excreted (Reynolds, Miranda, & Cumming, 2015; Viana,

Santamaría, & Figuerola, 2016; González-Varo *et al.*, 2017). Resource linkers transport nutrients and organic material, sometimes between ecosystems (Hannan *et al.*, 2007; Abbas *et al.*, 2012; Subalusky *et al.*, 2015). Lastly, process linkers 'transport' essential ecological processes into communities by moving between patches or habitats. These processes can relate to trophic interactions (the mobile link is then called a trophic process link), important examples being herbivores, predators, or parasites that exert pressure on certain plant or prey species and thereby influence population and community dynamics or their spatial patterns (Fuhlendorf & Engle, 2004; Avgar *et al.*, 2008a). Or these processes can influence the physiochemical environment by transforming material (non-trophic process links). For example, animals can provide disturbance to plants *via* trampling or uprooting (D'Souza *et al.*, 2015). The concept of non-trophic process links is similar to the concept of ecosystem engineers with a stronger focus on the 'engineering' species's movements that facilitate the process.

When considering the movements of mobile links, we must take care to distinguish between the scales at which their movements affect their own population dynamics and the scales at which they affect processes for other organisms and communities (often at other trophic levels). According to our organism-centered definition of scale (see Section II.1), the same absolute spatial distance might represent different scales for mobile links and the interacting species. For example, frugivorous birds may move locally to forage in different trees and disperse seeds *via* endozoochory (Morales *et al.*, 2013), whereby local foraging movements of a genetic linker result in regional dispersal movements of a transported organism. Thus, the same movement process can have population- and community-level implications at different scales when different (sets of) species are considered. Therefore, for all but dispersal movements, we distinguish direct effects and mobile-link effects of how movement impacts communities and coexistence (Table 1).

## (3) Community assembly, local and regional coexistence

The main processes that drive the structure of local communities are often conceptually viewed as step-wise passing (or failing to pass) of species from a regional species pool through multiple filters ('community assembly'; see lower panel of Fig. 1) (HilleRisLambers *et al.*, 2012; Kraft *et al.*, 2015). First, for a species to establish at a particular location, its dispersal abilities must be sufficient to reach the location (*dispersal limitation*). Second, abiotic environmental conditions must be suitable to allow survival and successful reproduction (*environmental filter*). Third, biotic interactions must allow persistence in the presence of other species when exploitation, interference or apparent competition but also trophic interactions pose further challenges (*biotic filter*). Note that we use 'community assembly' generally for the processes that shape community composition, in contrast to its original use in the sense of the sequential assembly of a community during,

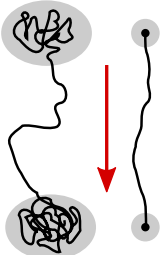
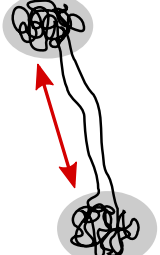
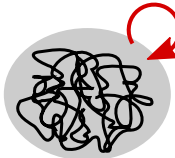
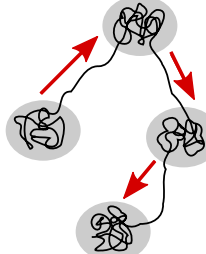


**Fig. 1.** The movement ecology framework for interacting individuals (upper part in blue), unified with major concepts from metacommunity theory, community assembly and coexistence theory (lower part in yellow) through multiple links (arrows). Square boxes depict processes, and rounded shapes represent patterns. In movement ecology, movement is seen as a behavioural process. By contrast, in community ecology, movement typically appears as species-level mobility, which emerges (dotted arrows) from the underlying movement processes of individuals, either as active mobility or passive mobility conferred by genetic mobile links and abiotic vectors. In addition, movements by resource and process links scale up to influence abiotic and biotic environmental conditions (R-P-generated external factors) that drive metacommunity- and community-level processes. Note: we omit all factors at the community level that are not directly related to movement.

e.g. the colonization by species of an island (Simberloff & Wilson, 1969; Diamond, 1975). Often, both abiotic and biotic environmental factors together shape the outcome of competition and can be difficult to disentangle empirically (Cadotte & Tucker, 2017). Therefore, Kraft *et al.* (2015) advocate the use of environmental filtering *sensu stricto*, which applies when species cannot tolerate abiotic environmental conditions even in the absence of other species.

Coexistence theory can be seen as stepping in after environmental filtering *sensu stricto* to elucidate outcomes of the joint action of biotic interactions and the abiotic environment (HilleRisLambers *et al.*, 2012). One of the cornerstones of coexistence theory is the concept of the ecological niche. While Eltonian and Hutchinsonian niches are defined as species-specific properties, modern coexistence theory (MCT) focuses on niche differences, which are achieved, for example, by species being

regulated by different limiting factors or responding differently to variation in common limiting factors (Chesson, 2000b; Letten, Ke, & Fukami, 2016; Barabás, D'Andrea, & Stump, 2018). This latter approach highlights the importance of stabilizing mechanisms that reduce niche overlap and induce negative frequency dependence of growth rates, thereby creating a rare species advantage. Niche differences are complemented by average fitness differences between species (recently termed competitive advantage by Barabás *et al.*, 2018) that encompass the competitiveness of species and their adaptedness to the environment. Equalizing mechanisms, by definition, reduce fitness differences and the extent to which stabilizing mechanisms are necessary for coexistence (Chesson, 2000b; Barabás *et al.*, 2018). However, this separation should not mislead one to think about niche and fitness differences as being independent.

Movement type & long-term pattern	Characteristic features and function	Spatial scale of community effect
<b>Dispersal</b> 	<p><i>Movement leading to gene flow. Typically, this is movement between natal and reproductive site (natal dispersal; once per lifetime) or between sites of reproduction (sometimes referred to as breeding dispersal; possibly multiple times per lifetime).</i></p> <p>Dispersal is an important mechanism for maintaining genetic diversity, both for actively and passively moving organisms. Passively dispersing organisms often have a specific life-cycle stage (e.g. spore, egg, seed) that is adapted to being transported by abiotic vectors (e.g. wind or water) or biotic vectors (genetic mobile links).</p>	<p>Direct effect:</p> <ul style="list-style-type: none"> <li>• Regional</li> <li>• Interregional</li> </ul>
<b>Migration</b> 	<p><i>Bi-directional movements between distinct breeding and non-breeding sites, which are often long distance in relation to body size.</i></p> <p>Migrating animals use seasonally variable resources or escape seasonal risks (seasonal migration; one to multiple times per lifetime), or complete their life cycle in different habitats, e.g. aquatic and terrestrial (life-cycle migration; once per lifetime). Outside the actual migratory phase, individuals may perform station-keeping or nomadic movement within their breeding and non-breeding range.</p>	<p>Direct effect:</p> <ul style="list-style-type: none"> <li>• Regional</li> <li>• Interregional</li> </ul> <p>Mobile-link effect:</p> <ul style="list-style-type: none"> <li>• Regional</li> <li>• Interregional</li> </ul>
<b>Station-keeping movement</b> 	<p><i>Daily movements within a restricted area (home range).</i></p> <p>Range-resident animals perform station-keeping movements throughout their lifetime, possibly excepting dispersal phases. Although home ranges can be dynamic in space and time, they are typically used throughout the reproductive lifetime of an individual. We also refer to station-keeping movements when migratory animals perform their daily movements such as foraging outside the migratory phase in restricted areas.</p>	<p>Direct effect:</p> <ul style="list-style-type: none"> <li>• Local</li> </ul> <p>Mobile-link effect:</p> <ul style="list-style-type: none"> <li>• Regional</li> </ul>
<b>Nomadism</b> 	<p><i>Undirected movements between irregularly shifting transient core areas (multiple times within months, a year, or a lifetime).</i></p> <p>Nomadic animals typically use resources that change irregularly in space and time. Nomadic movements between transient core areas are interspersed with daily local movements. In this way, some nomadic animals cover large distances during their lifetime. Nomadism may also occur seasonally, e.g. only during the non-breeding season. Nomadism differs from dispersal, as nomadic movements occur typically within a population rather than a metapopulation (see also Mueller &amp; Fagan, 2008).</p>	<p>Direct effect:</p> <ul style="list-style-type: none"> <li>• Local</li> <li>• Regional</li> </ul> <p>Mobile-link effect:</p> <ul style="list-style-type: none"> <li>• Regional</li> </ul>

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Often, both equalizing and stabilizing mechanisms operate simultaneously and possibly stem from the same ecological process (Barabás *et al.*, 2018).

Although initially developed to explain coexistence locally in temporally varying environments, coexistence theory was soon extended to spatially varying environments (Chesson, 2000a; Barabás *et al.*, 2018). Within this framework, it can help further to elucidate coexistence in competitive metacommunities. Metacommunity theory commonly distinguishes the four paradigms neutral, patch-dynamic, species-sorting, and mass effect. These paradigms take different, but not mutually exclusive, perspectives on how metacommunity structure is maintained. While the neutral paradigm attributes diversity to stochastic outcomes of emigration, immigration, extinction and speciation, the other paradigms highlight the roles of habitat heterogeneity and environmental filtering (species sorting), spatial dynamics *via* dispersal (mass effects), and trade-offs between local competitive and dispersal abilities (patch dynamics) (Leibold *et al.*, 2004; Logue *et al.*, 2011). Shoemaker & Melbourne (2016) showed that within these paradigms (except, by definition, in the neutral model), species coexistence at the regional scale can arise from a combination of non-spatial coexistence mechanisms (fluctuation-independent mechanisms, relative non-linearities, and the temporal storage effect; see e.g. Barabás *et al.*, 2018) and specific spatial mechanisms (fitness–density covariance, spatial storage effect).

One of the difficulties in applying modern coexistence theory to empirical processes and patterns is that its coexistence mechanisms are aggregated and conceptual and can arise from a multitude of ecological processes and organismal traits (Barabás *et al.*, 2018; Ellner *et al.*, 2018). Recent methodological advances may help to alleviate this problem in the future: Ellner *et al.* (2018) propose a framework in which long-term species growth rates – crucial to evaluate rare species advantages – are decomposed not necessarily into the canonical coexistence mechanisms of MCT, but into any ecologically relevant mechanisms, for example local retention of seeds, plant–soil feedbacks, or facilitation processes in the context of plant species coexistence. With a similar focus on concrete ecological mechanisms, we here consider organismal movement and resultant processes and how they affect species coexistence. However, where possible, we also report how these

effects fit into the equalizing–stabilizing paradigm of MCT.

### III. MOVEMENT-MEDIATED COMMUNITY ASSEMBLY AND COEXISTENCE

In the following, we review current knowledge on the relevance of individual-level movement processes on short time-scales for community processes and patterns on longer, ecological timescales. More specifically, we consider in turn the four basic movement types (Fig. 2), and how characteristics of the movement processes involved influence the community-assembly steps and coexistence mechanisms described above.

#### (1) Dispersal

Dispersal is key to metacommunity dynamics. Dispersal rates determine how strongly communities are connected and to which extent regional-scale diversity arises from spatial turnover through species sorting, local alpha diversities driven by mass effects, and heterogeneities in species dispersal (e.g. Logue *et al.*, 2011). From a local perspective, the metacommunity provides the regional species pool, from which local communities assemble, and a species' dispersal capacity determines whether it can colonize a suitable site and whether sink locations can be supported (local perspective of the mass effect). Thus, understanding dispersal processes and estimating dispersal rates and distances is paramount to understanding (meta)communities (Jönsson *et al.*, 2016). During recent years, it has been pointed out repeatedly that there are still methodological gaps in dispersal studies: they should more frequently embrace variability in dispersal among species (Heino *et al.*, 2015) and individuals (Cote *et al.*, 2010; Wey *et al.*, 2015), consider behavioural processes during the dispersal process (Auffret *et al.*, 2017), and quantify dispersal directly instead of using indirect proxies (Driscoll *et al.*, 2013; Keeley *et al.*, 2017). This calls for an integration of the movement ecology framework into dispersal studies (see e.g. McMahon *et al.*, 2014), linking it with the dispersal evolutionary ecology framework to account for the strong connection of dispersal with gene flow (Baguette, Stevens, & Clobert, 2014).

The movement ecology framework is particularly suitable to address questions about the transience stage of the

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**Fig. 2.** The four basic types of movement, which can be distinguished by different patterns that the underlying movement processes generate over an organism's lifetime (pictograms; variation possible) but also serve different ecological functions. The movement types occur at different spatial scales, where they have direct effects on moving focal species and their competitors, and may further confer mobile link functions to other organisms (typically at other trophic levels) at scales that differ from those of the direct effects. Note that here we follow a more general definition of dispersal, not necessarily limiting it to the strict uses of the terms natal and breeding dispersal. In this sense, dispersal may include, for example, a combination of movements related to foraging and reproduction (e.g. oviposition in insects) that results in an ultimate net dispersal away from the natal or a previous reproductive site (Clobert *et al.*, 2012). Pictograms adapted from Barton *et al.* (2015).

Table 1. Community-level impacts of movement. For each movement type, specific components and characteristics of the movement process scale up to patterns in mobility or abiotic and biotic external factors, which in turn affect metacommunity dynamics (i.e. the extent to which species sorting, mass effects and patch dynamics occur), the different steps of community assembly, and coexistence mechanisms (see also Fig. 1).

Movement type	Community-level impact	Relevant movement features	
		Emergent mobility or environmental pattern	Movement characteristics
Dispersal	<b>Direct effects</b>		
	Regional species pool	Frequency of long-distance dispersal events	Adaptation to long-distance dispersal (including distance)
	Metacommunity dynamics Dispersal limitation	Dispersal rate Dispersal distance	Motion capacity Orientation mechanism Habitat selection Internal state (e.g. exploration behaviour)
Migration	<b>Direct effects</b>		
	Regional species pool dynamics	Arrival time	Movement mode Travel speed Daily travel distance Stopover duration Orientation mechanism Habitat selection
		Route and destination sites	
	Niche differences	Migration <i>versus</i> residency	
	<b>Mobile-link effects</b>		
Station-keeping movement	Metacommunity dynamics (genetic links)	Dispersal rate	Migration distances
	Dispersal limitation (genetic links)	Dispersal distance	Use of stopover sites
	Abiotic environmental filter (resource links)	High or pulsed nutrient input	Migration as a strategy
	Biotic filter (process links)	Pulsed predation <sup>a</sup>	Migration as a strategy
	<b>Direct effects</b>		
	Niche differences: resource partitioning	Differentiation in mobility Spatio-temporal segregation	Movement rates and distances (within and between foraging arenas) Residence time (Micro)habitat selection Plasticity in movement strategy
	Interference and apparent competition	Spatio-temporal segregation	Fine-scale interspecific interactions (avoidance and attraction)
	Fitness similarity: energy trade-offs	Differences in mobility	Locomotion pattern Movement rates Movement distances
	<b>Mobile-link effects</b>		
	Metacommunity dynamics (genetic links)	Dispersal rate Dispersal distance	Recurrence in movement Movement rates Movement–physiology interactions
Nomadism	Environmental filter (resource links)	Local high-intensity space use and nutrient input	Recursive movement Residence time (Micro)habitat selection Fine-scale interspecific interactions (e.g. predator–prey)
	Metacommunity dynamics	Environmental spatial heterogeneity	Recurrence in movement Inter-patch movement rates
	Successional mosaics		
	Abiotic–biotic filter (resource and process links)		
	Niche differences: negative frequency-dependent growth (process links)	Distance- and density-dependent predation pressure	Orientation: response to cues
	<b>Direct effects</b>		
	Niche differentiation: resource partitioning	Nomadism as a strategy	Motion capacity
	Fitness similarity	Scale differences in foraging	Nomadism as a strategy

(Continues)



Table 1. (Cont.)

Movement type	Community-level impact	Relevant movement features	
		Emergent mobility or environmental pattern	Movement characteristics
	<b>Mobile-link effect</b>		
	Dispersal limitation (genetic links)		
	Dispersal rate	Movement distances	
	Dispersal distance	Habitat selection	
		Navigation: orientation mechanism	
Successional mosaics (process links)	Spatiotemporal disturbance pattern	Nomadism as a strategy	

<sup>a</sup>includes herbivory and parasitism.

dispersal process, although there exist links to the other stages (departure and settlement) (Baguette *et al.*, 2014). Transience is the most critical stage in determining final dispersal distances of an organism and hence the spatial scales at which dispersal limitation can manifest. Clearly, dispersal distances are influenced by motion capacities, which arise from the morphological and physiological traits of organisms or their dispersing propagules (De Bie *et al.*, 2012; McMahon *et al.*, 2014; Stevens *et al.*, 2014). In actively moving animals, dispersal distances tend to be larger with increasing body size and mass (Jenkins *et al.*, 2007; Stevens *et al.*, 2014), suggesting that an allometric scaling of movement (Carbone *et al.*, 2005) may hold for this particular movement type. For passive dispersal, the relationship between propagule size and dispersal distance is less clear (Jenkins *et al.*, 2007), possibly because of different vectors (abiotic and biotic). For microbes, Baas Becking (1934) coined the ‘everything is everywhere, but the environment selects’ hypothesis that was extended to claim no dispersal limitation for microscopic organisms. Although some taxa are indeed cosmopolitan with superb potential for long-distance dispersal (LDD) at inter-continental scales, many other taxa of microscopic organisms have restricted geographic distributions with presumably much lower potential for LDD (Fontaneto, 2019). The effect of biotic vectors is discussed in sections below. Dispersal distances are further influenced by internal motivations. Differences have been observed, for example, between habitat-specialist and generalist species, with specialists being less explorative and dispersing shorter distances than generalists (Stevens *et al.*, 2014; Dahirel *et al.*, 2015). Similarly, we also find differences within species among individuals with different personalities (i.e. behavioural dispersal syndromes; Cote *et al.*, 2010; Wey *et al.*, 2015).

During transience, dispersing organisms often cross unsuitable matrix, and their ability to survive and locate suitable habitat for settlement scales up, over many individuals, to affect dispersal rates (e.g. Lee & Bolger, 2017). While passively dispersing organisms usually cannot decide their exact dispersal routes, actively moving animals make movement

decisions in relation to environmental or other types of information (Clobert *et al.*, 2009; Knowlton & Graham, 2010). Navigation capacities can be crucial in locating habitat patches. While direct visual cues are used when inter-patch distances are not large (Ibarra-Macias, Robinson, & Gaines, 2011; Kay *et al.*, 2016), more indirect cues, such as conspecific density, prevail for dispersal over longer distances (Clobert *et al.*, 2009). Internal state can determine whether animals traverse hostile environments or barriers. For example, some studies have found that during movements through unfamiliar habitats, which is typical for dispersal, the willingness to enter less-preferred vegetation types is likely enhanced, which highlights the importance of collecting data from actual dispersal movements (Knowlton & Graham, 2010; Keeley *et al.*, 2017).

While in the previous paragraphs we argued that the details of dispersal movement processes crucially determine the outcomes of dispersal at the population level (e.g. distributions of rates and distances) and should thus be closer examined, an aggregated view of dispersal can still serve to understand diversity in metacommunities due to the large timescales involved. For example, allometric approaches to specifying species’ dispersal are useful to render biodiversity dynamics tractable in species- and interaction-rich meta-foodweb models (Ryser *et al.*, 2019). Also, species-specific heterogeneity in dispersal abilities has been investigated in the metacommunity paradigm ‘patch dynamics’ in the form of the colonization–competition trade-off (CCTO; high dispersal ability is linked with low performance in competition and *vice versa*). Trade-offs in ecological traits are a constituent part of coexistence-enabling niche differences (Kneitel & Chase, 2004), and CCTO works this out in a spatial dimension. Although the regional-scale CCTO is a well-known hypothesis [also in the ‘aggregation model of coexistence’, although in this model aggregation need not arise from differences in dispersal (Shorrocks, Atkinson, & Charlesworth, 1979; Sevenster, 1996)], its relevance in nature is not clear. While some studies that tested for this trade-off explicitly present evidence, mostly for organisms

that disperse passively or use ephemeral resources (Hanski & Ranta, 1983; Turnbull, Rees, & Crawley, 1999; Cadotte *et al.*, 2006), others failed to find support, possibly because of an insufficient ecological age of the studied system (Wilson, 2011; Pastore *et al.*, 2014). As a rare test on vertebrates, Rodríguez, Jansson, & Andrén (2007) found under field conditions that this mechanism appears to promote coexistence in a songbird guild (*Parus* spp.) in Sweden, where superior competitors were larger and inhabited predator-safe sites, whereas competitively inferior species were more mobile and could inhabit more isolated forest patches. Additionally, observed differences in dispersal distances in relation to dispersal syndromes as mentioned above might be related to CCTOs (Stevens *et al.*, 2014; Dahiré *et al.*, 2015; Cote *et al.*, 2017). Studies have classified CCTO as an equalizing or stabilizing mechanism (in the sense of MCT; Barabás *et al.*, 2018), often based on heuristic arguments, however, a rigorous analysis by Shoemaker & Melbourne (2016) revealed that CCTO has an equalizing and a stabilizing component: the better disperser benefits from intraspecific aggregation (representing reduced interspecific competition), while the better competitor suffers from it, balancing out *a priori* fitness differences.

In addition to driving population dynamics and community composition within metacommunities, dispersal movements – with all their abovementioned intricacies – are further important in driving species range distributions (Holloway & Miller, 2017). In this way, dispersal influences the size of a metacommunity, that is over which spatial extent connectivity can be maintained and species exchanged, similar to the idea of a regional species pool supplying local communities. At this possibly inter-regional scale, capacities for LDD are especially important, although LDD events tend to be rare and hence can drive regional processes only on longer timescales. This makes LDD more difficult to observe and quantify directly (but see Griesser *et al.*, 2014), but indirect evidence comes from genetic analyses. Although LDD events have been occasionally identified in actively moving animals, such as highly mobile wolves (*Canis lupus*; Vilà *et al.*, 2003), more studies on LDD are available for plants and invertebrates (Incagnone *et al.*, 2015) and invasive or otherwise harmful species (e.g. Ling *et al.*, 2009; Reynolds *et al.*, 2015; Ramos *et al.*, 2016). For plants, invertebrates and microorganisms, the mobility necessary for LDD can be conferred by large-scale wind or water currents but also highly mobile vectors (genetic linkers), especially migratory animals (Gillespie *et al.*, 2012; see Sections III.2b and III.4b).

## (2) Seasonal and life-cycle migration

Migration is a widespread phenomenon in animals. It has been studied widely, from an evolutionary and ecological perspective (Milner-Gulland, Fryxell, & Sinclair, 2011), and recently also from an ecosystem perspective considering transport and trophic effects of migratory animals (Holdo *et al.*, 2011; Bauer & Hoyer, 2014). We will consider in turn direct effects of migration within migratory animals' own

trophic level and guilds and mobile-link effects that usually apply to organisms at other trophic levels.

### a Direct effects

In our framework, the when and where of animal migrations directly affects regional species pools. While extinction and speciation drive species pools on relatively long timescales, migration produces inter-regional dynamics on much shorter timescales. According to the seasonal dynamics of migration, competition in communities tightens in pulses, with large consequences for species with strong resource niche overlap. When and where migratory species contribute to communities and elicit competition between residents and migrants or between multiple arriving migrants depends strongly on the environmental factors that drive migration (Milner-Gulland *et al.*, 2011; Teitelbaum *et al.*, 2015) but is also linked to the movement process of the migratory phase itself.

Most detailed movement data on migrations are available for birds, among which a fifth of all species are migratory (Somveille *et al.*, 2013). Spring arrival times of migrants are critical in competition for nest sites and territories and early arrival can be achieved either through fast migration or short migration distance (Kokko, 1999; Visser *et al.*, 2009; Nilsson, Klaassen, & Alerstam, 2013). Migration speed is related to flight mode, flapping being more energetic costly than soaring but also less dependent on weather conditions and less prone to off-route drift, hence being more suitable for a time-minimization strategy during migration. Other factors in flight behaviour that support fast migration are the daily travel distance, which can be increased by higher speeds, longer flight duration, and particularly the total duration of stopovers during the journey, which can be reduced by night-time flight (allowing daytime foraging) or a combined flight-and-forage strategy (Nilsson *et al.*, 2013). Findings that birds employ such strategies predominantly during spring migration have been mostly linked to intraspecific competition, however, they may similarly apply to interspecific competition. For example, cavity-nesting bird species experience strong competition for a limited number of nest sites, such that early spring arrival of migrants can be beneficial for occupation of nest sites (Alerstam & Högstedt, 1981). However, early arrival also increases direct interference competition with residents (Ahola *et al.*, 2007). As arrival times are furthermore strongly linked to food availability, this creates a complex optimization problem, in which movement-related decisions are one means to enhance competitiveness (Schaefer *et al.*, 2018).

In which regions or locations migratory species supplement resident communities depends mostly on movement–environment interactions but also, proximately, on navigation strategies. The regions between which migratory animals travel can be fairly fixed. However, some individuals may serve as innovators in establishing new migration routes and off-migration sites (e.g. wintering sites). These innovations may be driven by inexperienced individuals that have only crude navigation capacities and are therefore subject

to high stochasticity in travel destination (Cresswell, 2014), or by experienced older individuals that can identify new sites with suitable habitat (Teitelbaum *et al.*, 2016). Observations of events where new migratory routes lead to population-level effects in a newly established site are difficult to make and usually only possible retrospectively. One such example is the over-wintering of south-central European blackcaps (*Sylvia atricapilla*) in the British Isles since the 1960s, representing migration in an entirely new compass direction (Bearhop *et al.*, 2005; Hiemer *et al.*, 2018). However, we are not aware of any reports on novel competitive interactions between the blackcaps and resident species at these locations.

The evolution of seasonal migration as a strategy complementing residency (and also partial migration) has sparked much interest. Related to this is the question how the strategies coexist thereby allowing species coexistence. Theoretical studies support the ubiquity of migration, showing that both migration and residency can invade each other in most scenarios of environmental seasonality (Holt & Fryxell, 2013). A possible explanation for this is that migrant and resident populations are regulated by different factors, predation typically playing a larger role for residents and resource availability being a stronger limiting factor for migrants (Fryxell & Sinclair, 1988; Holdo *et al.*, 2011). Such different regulating factors have been put forward as an explanation for the high relative abundance of migratory ungulates in various ecosystems (Fryxell, Greever, & Sinclair, 2002). Similarly, if residents are limited by predation and food availability during the breeding season and migrants are limited by food availability during the non-breeding season, coexistence can occur in tropical bird communities even during periods of low food abundance (Johnson, Strong, & Sherry, 2006). In this sense, migration fosters niche differentiation between species, drawing both on spatial and temporal variation in environmental conditions. It would be interesting to investigate whether one could understand this conceptually in a similar way as coexistence mechanisms of MCT that draw on either spatial or temporal fluctuations in the environment. A good starting point are studies on the ecological drivers and the maintenance of partial migration within species, as similar concepts may work for the coexistence of migration and residency between species (Chapman *et al.*, 2011). Interestingly, partial migration is common among migrants, adding the question on the role of trait variation (see also Section IV).

#### *b Mobile-link effects*

As genetic, resource and process linkers, migratory animals couple ecosystems across biogeographic scales (Bauer & Hoyer, 2014). From a metacommunity perspective, migratory genetic linkers mainly function over large scales, connecting (meta-)communities across regions and continents (see Section III.1). This has been investigated especially for freshwater organisms (Baas Becking, 1934; Incagnone *et al.*, 2015). Microorganisms as well as plant propagules can be transported by waterfowl both *via* endo- and ectozoochory.

Although the effectiveness of biotic vectors over physical vectors may be case specific (Incagnone *et al.*, 2015), birds have been identified as drivers of LDD in aquatic species (Reynolds *et al.*, 2015; Viana *et al.*, 2016). Because of their longer distances, migratory movements of waterfowl species are particularly important for LDD (Viana *et al.*, 2016). Given limited gut passage times, more important than migration distances *per se* may be the use of stopover sites, including temporary water bodies that constitute reservoirs of biodiversity (Incagnone *et al.*, 2015).

Further transport effects are provided by resource links. A classic example is spawning salmon that return in large numbers to freshwater streams, where they die. Their carcasses are carried away from streams by predators and scavengers and provide significant nutrient subsidies into riparian areas, lessening the effect of abiotic filters relative to biotic filters for primary producers, reduce species richness and shift community composition (Hurteau *et al.*, 2016). The significance of migration for this community-level effect lies in allowing nutrient transfer between distant ecosystems. *Via* migration, salmon utilize the nutrients of marine environments for growth while using freshwater streams as a relatively safe spawning habitat, where they ultimately deposit nutrients. Similarly, migrating sea turtles transport substantial amounts of nutrients large distances from foraging grounds to nesting grounds, where they fertilize dune plants (Hannan *et al.*, 2007). A slightly different case is migratory seabirds, which are known to enhance nutrient levels critically in the terrestrial systems on their breeding islands (Bauer & Hoyer, 2014). Here, it is rather station-keeping movements during the breeding season that allow the nutrient transfer (see Section III.3); however, migration is important in allowing the birds to utilize these specific regions during the breeding season.

Similar considerations as for resource linkers hold for trophic process linkers. Migratory animals can have strong effects on other trophic levels by providing pulses of herbivory, predation, or parasitism in addition to the permanent background consumption of resident species, or by serving as temporarily available prey themselves [see Bauer & Hoyer, 2014 and references therein]. These effects occur usually at destination sites of migration (Popa-Lisceanu *et al.*, 2007), and therefore the migratory movement mainly serves simply to procure them seasonally. More direct interactions between movement processes during migration and trophic-link effects remain to be investigated.

### **(3) Station-keeping movements**

#### *a Direct effects*

Differences in the characteristics of station-keeping movements can allow competing mobile species to reduce both exploitation and interference competition as well as to use trade-offs in energy regulation to balance out competitiveness. A starkly contrasting dichotomy in foraging modes exists between ambush (or sit-and-wait) and actively

searching predators. These two foraging modes arise as clusters of movement traits, possibly coevolved (Cooper, 2007), whereby active foragers typically show higher average movement speeds and spend more time moving than ambush foragers. Compared to ambush hunting, active foraging often leads to higher prey encounter rates but incurs greater movement costs (Scharf *et al.*, 2006; Avgar *et al.*, 2008b). This trade-off might allow species with different foraging modes to balance out net energy gains (equalizing effect). When foraging strategies are additionally linked to different prey types, the contrast can also have a stabilizing effect on the predator species *via* resource partitioning (Nakano, Fausch, & Kitano, 1999). However, there might even be a third way in which dichotomic movement strategies promote coexistence when we additionally consider prey movements. Modelling studies suggest that predator foraging success depends not only on their own movement rates but also on the interplay of their own and prey movements: higher encounter rates of active searchers rely on predators moving faster than prey, or prey moving with low levels of directionality (Scharf *et al.*, 2006; Avgar *et al.*, 2008b). Empirical studies in a spider–grasshopper system show that prey, in turn, adjust their movement rates to the mobility of their predators (Miller, Ament, & Schmitz, 2014). Thus, a predator's mobility level might induce prey mobility levels that support the opposite predatory strategy, such that a rare predator strategy can have an advantage (stabilizing effect).

Similar albeit less starkly contrasting foraging patterns exist in herbivores, which can also be linked to trade-offs between food intake and movement-related costs (including predation risk) and simultaneously lead to partially exclusive resource use. For example, two similar folivorous lemur species (*Avahi occidentalis*, *Lepilemur edwardsi*) express different locomotion patterns, where the wider ranging species performs more energy-demanding leaps between trees but forages more selectively and takes higher quality food (Warren & Crompton, 1997). Another example are African ungulate guilds, in which different patterns in terms of within-patch displacements as well as movement rates and durations between patches are linked to spatiotemporal segregation of species (Macandza *et al.*, 2012; Owen-Smith, Martin, & Yoganand, 2015). Such partitioning in resource use *via* behavioural differentiation may operate at relatively small spatial scales, not being evident at home range scale but becoming apparent when zooming in on movements with greater temporal resolution.

Spatiotemporal segregation at fine scales can also arise through active avoidance between heterospecific individuals. This can be effective in reducing interference competition between (meso-)predators (Nakano *et al.*, 1999; Vanak *et al.*, 2013) or avoiding a shared predator (Macandza *et al.*, 2012). Fine-scale avoidance occurs at the scale of individual movement decisions, and we expect this to be strongly influenced by internal state (e.g. risk-taking propensity) and navigation capacity (e.g. sensing and memory). Whether this

mechanism in the long term may mainly reduce a dominant species' competitive advantage over subordinate species or can also manifest in niche differentiation remains to be investigated.

#### *b Genetic-link effects*

Station-keeping movements further affect the dispersal movements of other organisms, thereby serving as genetic mobile links. Metacommunity effects for the transported organisms (e.g. whether dispersal rates promote species sorting or mass effects) depend most importantly on genetic linkers' movement rates and distances. While animals that travel longer distances on a daily basis, for example larger animals, tend to favour LDD, highly active species that move frequently between different foraging sites facilitate higher dispersal rates (Nathan *et al.*, 2008b; Schwalb, Morris, & Cottenie, 2015). Many animals concentrate their feeding in multiple, spatially distinct core areas within their home ranges, sometimes in fairly regular patterns (Berger-Tal & Bar-David, 2015). When such animals act as biotic vectors for organisms or their propagules, this may lead to the high dispersal rates necessary to maintain mass effects (Heymann *et al.*, 2017). Animals vary their mobility patterns, for example seasonally, such that realized dispersal might deviate from predictions based on general estimates of a vector's movement ability (Ismail *et al.*, 2017). Also, when assessing the dispersal potential of propagules *via* endozoochory, movement distances and patterns are not only important *per se*, but also in influencing the digestive processes. For example, movement distances of mobile linkers must be linked with gut retention times to obtain estimates of dispersal, but combining independent measures of the two is not enough, as mobility levels significantly affect retention times and hence both dispersal distance and propagule survival (van Leeuwen *et al.*, 2016).

Although highly active mobile linkers have the potential to build strong links between certain patches, a single mobile-link individual or even species will unlikely be able to provide complete connectivity to a metacommunity. Each species, and even individuals within species, will link patches in correspondence to their resource requirements and preferences and in response to the available landscape structure, selecting different sites, and moving between sites with varying frequency and time lags (Carlo *et al.*, 2013; Morales *et al.*, 2013). On the one hand, when the link between an organism and its vector is strongly specific, this may promote differences in dispersal that scale up to a dispersal–colonization trade-off. On the other hand, when organisms can be transported by multiple vectors with differing movement behaviours, this can result in overall more evenly distributed dispersal patterns. This has been demonstrated for interactions between frugivorous birds and seeds, where a diverse frugivorous community with different space use and movement patterns produces complementary seed rains (González-Varo *et al.*, 2017).

### c Resource- and process-link effects

Foraging movement patterns of resource linkers and trophic linkers can have both local and regional effects by influencing the external environmental conditions that other organisms experience. Locally, repeated high nutrient input by resource linkers at local sites may affect the abiotic environmental filter that operates during community assembly. At the one end, intense nutrient loading can cause abiotic conditions that are not tolerated well by many species. For example, animal excreta enhance dissolved-oxygen depletion and ammonium levels in aquatic systems, which can be detrimental to fish (Wagner, 1978). At the other end, in extremely nutrient-poor systems, organic input from mobile links can decrease the strength of the environmental filter and allow greater diversity, which, for example, appears to occur for islands and surrounding shallow banks that receive nutrients through excreta from seabird colonies (Powell *et al.*, 1991). The emergence of spatially concentrated nutrient subsidies requires particular movement behaviours such as strong localized habitat selection or defecation, for example, as performed by grazers that evade high temperatures by repeatedly spending much time in the same riparian areas (Allred *et al.*, 2013; Earl & Zollner, 2017). Additionally, unidirectional ‘conveyor belts’ for nutrients result from daily recurrent movements between areas of nutrient uptake and loss, e.g. feeding and resting places (Abbas *et al.*, 2012; Subalussy *et al.*, 2015). Even when vector movement is less regular, aggregated resource input can arise indirectly, for example, when predator–prey spatial interactions lead to clusters of prey carcasses (Bump *et al.*, 2009). Nutrient subsidy by mobile links also contributes to local community structuring through secondary effects. High site fidelity of aggregating mesopredatory fish attracts grazers (trophic linkers) that provide strong herbivory pressure, suppress macroalgae and thereby facilitate coral settlement and survival (Shantz *et al.*, 2015). Note that, although local mobile-link effects can be strong enough to affect environmental filtering *sensu stricto*, they often create changes in external conditions that interact with biotic factors (e.g. competition effects) to shape local communities.

Recurrence in movement patterns of resource and process links, especially herbivores that often act as both, also plays a role by creating spatial and spatiotemporal heterogeneity in external conditions. Such heterogeneity is the basis for species sorting in metacommunities but also for spatial variation in competitive abilities that supports the spatial storage effect and mass effects (Mouquet *et al.*, 2002; Sears & Chesson, 2007) or enhances the chance for coexistence *via* CCTO (Cronin, Loeuille, & Monnin, 2016). Additionally, recurrent movements by resource or process links contribute to successional mosaics that are caused by spatiotemporal dynamics in disturbances (allogenic disturbance *sensu* Wilson, 2011). Which type of patterns occur depends on the frequency of repeated visits to the same foraging sites, but also on feeding behaviour. When grazing or browsing is selective, frequent visits to the same preferred patches lead to arrested

succession (‘cultivation grazing’; D’Souza *et al.*, 2015). Such patches maintain primary successional plant species, which can create a contrast with the surrounding landscape if this is dominated by later successional species (Olofsson, de Mazancourt, & Crawley, 2008). By contrast, generalist herbivores that provide strong disturbance but revisit areas more rarely rather create shifting mosaics of patches at different successional stages (Sommer, 1999; Fuhlendorf & Engle, 2004).

Another important aspect of the foraging movements of trophic linkers can be their navigation capacities and the way in which they respond to cues. Predators, including herbivores, that exert density- or distance-dependent mortality, while being sufficiently prey specific, contribute to negative frequency-dependent growth of their prey [pest pressure *sensu* Wilson, 2011; Janzen–Connell effect (Janzen, 1970); Fricke, Tewksbury, & Rogers, 2014]. Clearly, foraging behaviours of predators contribute to mortality patterns, as animals often focus search efforts where they expect high food abundance. However, it may not be that simple: for example, in contrast to a solitary foraging ant (*Messor arenarius*) that only responded to resource density, a socially foraging ant (*Messor ebenius*) that also responded to cues from conspecifics was able to generate seed survival patterns in line with Janzen–Connell predictions (Avgar *et al.*, 2008a).

### (4) Nomadism

Of the four movement types, nomadism is the least investigated. This may be due partly to conceptual difficulties in setting it apart from migration and station-keeping, which have been amended by Mueller & Fagan (2008), but also to challenges in tracking the movements of nomadic animals. Their large scale and irregularity render some methods more difficult, such as radio-tracking or the use of data loggers that need to be retrieved. However, reports of nomadism exist for various taxa (Teitelbaum & Mueller, 2019), and we here synthesize currently known aspects of nomadism for community ecology.

#### a Direct effects

Similar to migration, nomadism can be seen as a strategy complementing residency that promotes niche differentiation among species, whereby nomads have shifted their foraging niche to unpredictably variable or ephemeral resources. For example, the movement behaviour and foraging niches of two sympatric wading birds, wood stork (*Mycteria americana*) and white ibis (*Eudocimus albus*), in the southeastern USA indicate that they have specialized on different strategies despite having similar feeding behaviour (Kushlan, 1981). Although inhabiting dynamic wetlands with high unpredictability in overall prey availability, wood storks use the same breeding colonies over long periods of time, facilitated by their strong flight abilities that allow them selectively to exploit the most stable water sources on a daily basis (Frederick & Ogden, 2006). White ibises, by contrast, rely on

shorter daily foraging trips and more unpredictable water sources, which impels them to nomadism and relocation of their breeding colonies according to yearly fluctuating food availability (Frederick & Ogden, 2006). This example demonstrates that nomadism is not always linked to strong movement capacities and large movement distances over the short term. More generally, Allen & Saunders (2002) suggest that nomadism is related to scale breaks in landscape and resource-availability patterns. In this sense, nomadic animals would be competitively inferior at each spatial scale on its own but are able to switch back and forth between them, for example seasonally (Lenz *et al.*, 2015). As such, nomadism could act both to facilitate resource partitioning and to equalize fitness across species.

#### *b Mobile-link effects*

Nomadism in frugivores and nectarivores can be central to their role as seed dispersers and pollinators. A straightforward benefit of nomadism is that it provides a chance for pollination or dispersal events over longer distances than most station-keeping movements. Additionally, nomadic foraging can be essential in facilitating seed dispersal in highly patchy habitats. For example, trumpeter hornbills (*Bycanistes bucinator*) that are nomadic during the non-breeding season visit fruiting trees much further into agricultural landscapes than during the breeding season when they remain in larger, continuous forest areas. They thus provide important connectivity for small forest patches in the agricultural matrix and ease dispersal limitation (Lenz *et al.*, 2015). A further critical aspect of nomadic foraging for seed dispersal can be its underlying navigation mechanism. To locate unpredictable resources, nomadic animals cannot rely on the innate fixed orientation mechanisms that are known to be important in migration. Instead, they rely on sensory stimuli from the environment, whereby sociality and large group sizes are important in facilitating effective search (Milner-Gulland *et al.*, 2011). Large group size, in turn, has been found to be crucial for effective seed dispersal by fruit bats (*Pteropus* spp.), as strong intraspecific interactions force individuals to carry fruits away from the tree (Eby *et al.*, 1999; McConkey & Drake, 2006).

The link between nomadism and large group size may also be important for other ecosystem effects of such animals. Large herds of herbivores exert strong effects on plant communities, through trophic and non-trophic (e.g. disturbance) effects. While ecosystem effects of natural nomadic movements of herding ungulates such as Mongolian gazelles (*Procapra gutturosa*; Mueller *et al.*, 2011) remain to be investigated, movements of domestic livestock or wild game in rangelands have received more attention. In systems where management objectives focus on increasing livestock productivity through steady-state management that confines movements, vegetation tends to become homogenized, accompanied by a shift towards pioneer or unpalatable species (Little, Hockey, & Jansen, 2015; Fuhlendorf *et al.*, 2017). More recent approaches recognize the importance of maintaining or reinstating spatiotemporal grazing regimes

through nomadic-like movements in order to preserve shifting-mosaic patterns of vegetation structure and resulting diversity of species that locally use these habitats (Augustine & Derner, 2015; Fuhlendorf *et al.*, 2017).

## IV. COMMUNITY PERSPECTIVE

The biggest hurdle in integrating movement and community ecology arises from a difference in perspective. The movement ecology framework (Nathan *et al.*, 2008a) highlights movement as an individual-level behavioural process, with variation in inner states and movement capacities and also in relation to individually experienced environmental conditions. By contrast, community assembly and coexistence theory usually average out individuals and focus on populations that are characterized by their means, for example long-term average population growth rates (Chesson, 2000b). Consequently, within this perspective, movement is usually represented by few species-level characteristics, such as average movement rates or distances, or dispersal kernels. The conceptual differences between movement ecology and community ecology likely also arise because of the large range in timescales that they cover. While movement processes occur within individual lifetimes, community-level effects play out over many generations. Truly to integrate movement and community ecology, we must reconcile the individual-based and population-based perspectives.

We propose that we can link the community assembly and coexistence framework, including metacommunity dynamics, with the movement ecology framework by using the concept of ‘micro–macro links’ (borrowing a term from sociology; Coleman, 1986). This concept refers to the fact that any structure and dynamics at the population or higher level emerges from the behaviour and decisions made by individual organisms, but the population-level features in turn affect the options and thus the behaviour of individuals, which is by no means a new idea in ecology (Sutherland, 1996; Grimm & Railsback, 2005). To capture this link, it is important to learn how behaviours emerge from the individuals’ adaptive decision-making, for example in response to changes in habitat or local density of conspecifics. At which level of detail this is integrated into studies of communities and metacommunities, however, depends on one’s question or objective. Using aggregated results of movement processes, for example at the population or species level, can help to cross scales and focus on mechanisms that play out at the community level (see the example of colonization–competition trade-offs in Section III.1). If the aim is prediction, such as predicting the response of organisms to new conditions, it may be unconstructive to impose behaviour *via* fixed parameters or rules, because imposed parameters are typically linked to the conditions under which they were observed (Grimm, Ayllón, & Railsback, 2017). However, when predicting large systems, involving many species and large spatial or temporal scales, such as in species distribution

modelling, employing species-level parameters can serve to attain model manageability and reduce computational burden. Establishing those parameters as emergent behaviours can then be an important step in the process, e.g. informing model components in hybrid or mechanistic species distribution models (Singer *et al.*, 2016).

In our framework, two broad types of patterns emerge from movement (Fig. 1, middle oval). First, *mobility* encompasses population-level movement patterns that emerge from movement processes within individual lifetimes. This also applies to passive mobility conferred by genetic links and abiotic vectors. As illustrated in detail above, species' mobilities, at ecological timescales, influence their dispersal rates within metacommunities, their degree of dispersal limitation at local sites, their differences in competitiveness, and niche differences (Table 1). Similarly, out of movement processes of mobile resource and process linkers emerge *patterns in abiotic and biotic external factors* (Fig. 1, Table 1), where biotic external factors include competitors, disturbance regimes, or predation pressure. At the community level, these abiotic and biotic conditions modify environmental filters (both *sensu stricto* and in interaction with biotic filters) and likewise affect competitive biotic interactions by serving as limiting factors to species in the focal community. Importantly, intra- and interspecific interactions occur on both timescales. Within individual life times, that is at the individual level, organisms can interact, for example by avoiding each other or by seeking each other out, both within and across trophic levels. These interactions, when viewed across many individuals, scale up to species-level interactions over ecological timescales, that is the population-level effects that species have on their own growth rates and those of other species. Therefore, understanding the effects of individual-level interactions on movement processes is essential because they in turn lead to the emergence of species-level interactions that determine coexistence and patterns of diversity.

Adopting the behaviour-based perspective on movement also opens the door to a better incorporation of variation in the environment, in individuals, and in environment–individual interactions into community ecology. Movement processes depend strongly on external factors, and will change in space and time as environmental conditions change. In addition, considerations of individual trait variation (ITV) and personality have recently started to perforate the classic mean-field approach (Turcotte & Levine, 2016; Spiegel *et al.*, 2017). While it is not clear whether variation among individuals generally facilitates or hampers coexistence (Bolnick *et al.*, 2011; Hart *et al.*, 2016), intraspecific trait variation is omnipresent, particularly in movement-related traits, and these differences affect the manifestation of intra- and interspecific interactions (Wolf & Weissing, 2012; Spiegel *et al.*, 2017; Schirmer *et al.*, 2019). Given the multiple sources of trait variation among individuals, it is important to scrutinize assumptions of well-mixed populations, to investigate how variation in movement processes scales up to variation in mobility- and mobile-link-generated patterns, and to incorporate this variation at the community level.

## V. CURRENT CHALLENGES AND AVENUES FOR FUTURE RESEARCH

### (1) Generating new data

Currently, the biggest leap in data acquisition is possible in the quantification of movement processes. Improvements in animal-tracking technology, such as global positioning system (GPS) devices, allow us to observe individuals' movements with increasing accuracy and resolution (Kays *et al.*, 2015; Weller-Weiser *et al.*, 2016), while auxiliary data from bio-logger sensors (e.g. accelerometers, thermometers, and microphones) provide us with an increasingly comprehensive picture of the conditions that animals experience during their movements (Wilmers *et al.*, 2015). However, due to the weight of animal-borne devices, these technologies are still limited mainly to vertebrate species. For example, high-resolution terrestrial tracking is currently available with tags of approximately 1 g that are suitable for animals down to 20–30 g body mass, depending on species-specific maximum acceptable weights of tags (López-López, 2016; Weller-Weiser *et al.*, 2016; Duda *et al.*, 2018), while acoustic tagging of fish or geolocation (e.g. for migratory birds) is possible with tags weighing as little as 0.3 g (López-López, 2016; Whoriskey & Hindell, 2016). Advances in stretching these limits further down are to be expected. Still, movement data of even smaller vertebrates or insects have until recently been obtained mainly through mark–recapture (e.g. Perry *et al.*, 2017) or by direct observation of marked moving individuals (Kay *et al.*, 2016; Brown *et al.*, 2017), limiting the scope and quantity of such data. Promising new avenues are automated radio-telemetry systems (Taylor *et al.*, 2017), improvements in tracking based on radio-frequency identification (RFID) (e.g. for insects; Barlow, O'Neill, & Pavlik, 2019), as well as image-based tracking (Dell *et al.*, 2014) and radar monitoring (Shamoun-Baranes *et al.*, 2014), the latter two methods not requiring any animal-borne tags and thus being suitable for small invertebrates (Augusiak & Van den Brink, 2015). However, radar- and image-based methods still have to solve the problem of distinguishing species and individuals (Dell *et al.*, 2014; Shamoun-Baranes *et al.*, 2014). Machine-learning-based classification of multiple simultaneously moving individuals might help to overcome this challenge (Pennekamp, Schtickzelle, & Petchey, 2015).

Our abilities for indirect inference of movement and dispersal processes by means of genetics has likewise greatly improved. Technological advances, both regarding DNA amplification and subsequent sequencing, enable relatively cheap screens of individual genotypes in multiple organisms at multiple loci, with recent next generation sequencing (NGS) even at a genomic scale. Provided a reasonable percentage of a population can be sampled, multilocus genotyping allows for characterization of individual genotypes. With such information, direct measurements of movement can be gained by two approaches, i.e. genetic mark–recapture of the same individual at different places ('genetic tagging'; Palsbøll *et al.*, 1997) or genetic identification of parent–offspring pairs

(Tiedemann *et al.*, 2017). For such analyses, minimal invasive (biopsy) or non-invasive (hairs, feathers, and faeces) sampling can be applied, as demonstrated in the inference of Eurasian otter (*Lutra lutra*) movements from genotyping otter spraints (Prigioni, Remonti, & Balestrieri, 2006). Furthermore, genetics can provide indirect estimates of dispersal by estimating gene flow among populations. With the advent of NGS techniques, such studies now overcome the limitations of earlier single/few loci studies and frequently target single nucleotide polymorphisms (SNPs) across individuals on a genomic scale (e.g. Lah *et al.*, 2016). In conjunction with new data analytical approaches [such as approximate Bayesian computation (ABC) or the software programs LAMARC and MIGRATE-N], such data allow for precise estimation of even asymmetric dispersal under non-equilibrium conditions (see Waples *et al.*, 2018). Additionally, contaminant or stable isotope signatures can be used to infer information on movements indirectly. This method works especially well for large-scale movements such as migration across continent-wide so-called isoscapes (Courtiol & Roussel, 2017), but may also be sufficient for tracking the origin of smaller organisms with limited motion capacities (Dammhahn, Randriamoria, & Goodman, 2017).

While these methods for indirectly inferring movements are also useful for actively moving organisms, mainly regarding dispersal (e.g. Tiedemann *et al.*, 2017; but see Prigioni *et al.*, 2006), they are to date the main approach for passively dispersing organism, such as plants (Auffret *et al.*, 2017) and microorganisms (Choudoir *et al.*, 2018). More direct methods would involve the collection of wind-dispersed propagules in air samples (Fernández-Rodríguez *et al.*, 2014) and the collection of dispersal stages directly from dispersal agents (Reynolds *et al.*, 2015). These techniques can utilize morphological or genetic species assignment and allow for extensive analyses of communities, but obtaining individual-level data is a challenge for microbes: for fungi and other modular organisms, there is not a clear definition of 'individual'. In bacteria, clonal organisms with often very high cell division rates, following an individual cell may not even be desirable.

Despite the relative ease with which we can track larger animals, we still see gaps in the design of studies. While comparative studies can reveal movement-related differences among species, which may foster coexistence within their communities (Conners *et al.*, 2015; Owen-Smith *et al.*, 2015) or within communities that they serve as mobile links (Morales *et al.*, 2013), *post-hoc* comparisons are difficult, because results of movement analyses often depend strongly on data-collection methods (e.g. sampling intervals; Rosser *et al.*, 2013). Therefore, we advocate recording movements of multiple species with the same protocol. Furthermore, simultaneous multi-individual and multi-species tracking is necessary to understand interactions better at the movement level. For example, interference competition may be reduced if competitors avoid each other in their fine-scale movements. Although this has been suggested as coexistence mechanism, few studies have investigated it (Vanak *et al.*, 2013). Exploring interactions, however, requires sufficiently detailed tracking

data. A recent promising development aimed at closing these gaps is the ATLAS system, capable of tracking multiple individuals of relatively small species in the same region at high spatiotemporal resolution (Weller-Weiser *et al.*, 2016). Moreover, most tracking studies on macroorganisms focus on station-keeping movements while paying less attention to dispersal. One reason may simply be greater investment required, for example, when only a small portion of individuals in a species disperse and thus many individuals need to be tagged. However, information on animal responses to habitats during foraging cannot always be transferred to dispersal movements (Keeley *et al.*, 2017), thus explicit observation of dispersal processes is desirable. Here, the forthcoming ICARUS tracking system (<http://www.orn.mpg.de/ICARUS>) will hopefully enable large-scale tracking of dispersing individuals of relatively small vertebrates.

At the interface of movement and community ecology, openly available, rich databases offer new opportunities for the integration of the two fields. Movement data can be found on platforms such as Movebank (Kranstauber *et al.*, 2011) and OzTrack (Dwyer *et al.*, 2015), while plant and animal occurrence data can be found, for example, on the Global Biodiversity Information Facility (GBIF) or on regional databases. Other databases such as LEDA (Kleyer *et al.*, 2008) or 3D Dispersal Diaspore Database (Hintze *et al.*, 2013) offer information about plant dispersal features (e.g. seed characteristics) which help to integrate biodiversity data with species' mobilities (through pollen or seeds) or mobile links' (pollinators and dispersers) mobilities. However, massive heterogeneity of the data in terms of quality, scales and types of measurements makes them difficult to integrate. Moreover, many classical data-collection methods are species specific and limited to certain movement or activity patterns, and hence may distort our knowledge of biodiversity. For example, light capture of nocturnal insects causes bias in trapped species and individuals, leading to an overrepresentation of phototactic species over species that avoid light or reduce activity in response to illumination, and of individuals with stronger flight-to-light behaviour, e.g. males or individuals during migration (Baker & Sadovy, 1978; Altermatt, Baumeyer, & Ebert, 2009; Eccard *et al.*, 2018). We therefore advocate an integrative framework for linking different data types and standardizing data collection, for example, through increased collaboration among taxon specialists and comparative sampling designs for biodiversity monitoring that guarantee a consistent long-term application of sampling methods. Such joint efforts will allow us to connect movement and community processes better.

## (2) Performing novel experiments

While the technical options to observe organismal movement in the field are rapidly increasing, identification of both underlying mechanisms of specific movement patterns and their consequences at the community level is still challenging. In principle, sound scientific experiments are the best option to unravel links between causes and consequences. However,



performing reproducible experiments on movements in natural environments is difficult. One reason is the gap in time-scales between short-term movement processes and possible consequences at the level of populations or communities. Other problems include the protection status of many larger animals, which limits the possibility for manipulation, logistic and financial challenges to conduct *in situ* landscape-scale experiments, and difficulties to tailor experimental manipulation to movement without affecting other aspects of behaviour.

An opportunity for such experiments under laboratory conditions is the automated image-based tracking of small multicellular organisms such as insects and zooplankton (Watt & Young, 1994; Dell *et al.*, 2014; Colangeli *et al.*, 2019). The small spatial scale, the relative ease with which these organisms can be reared in the laboratory, and their short generation times render manipulations in controlled conditions possible. For example, we can use such set-ups to study movement patterns across major feeding types (e.g. primary producers, consumers, and predators), or to investigate links between physiology and movement ecology (e.g. changes in movement characteristics of zooplankton with increasing temperature or changing resources), where experimental studies can complement biomechanical modelling approaches (Hirt *et al.*, 2017). In addition, experimental micro-landscapes can be designed to investigate effects of movement on coexistence of multiple species and even be extended to the community level. For example, microfluidic systems can be tailored to reflect fine-scale habitat characteristics to study movement within such spatial features as would occur in a soil matrix (Alekkett *et al.*, 2018). The small scale allows us to measure community effects of movement in experiments, with the potential to scale up or at least to compare those movement effects to communities at larger scales.

Even in real landscapes, certain aspects of small-scale laboratory experiments could be performed, using local multi-species tracking systems such as automated telemetry systems or ATLAS (see Section V.1). These systems allow for tracking many organisms of different species at a high temporal and spatial resolution. Ideally, they can be combined with manipulations of land use (e.g. mowing of grasslands or illumination to create risk landscapes or disturbances; Hoffmann, Palme, & Eccard, 2018) or landscape elements (e.g. through paid experimental management by farmers). These approaches of combining and systematically comparing different scales would stimulate the hybridization of well-established but currently separate disciplines.

### (3) Developing statistical tools

While we collect more detailed data on movements, another challenge is to keep up with statistical and computational tools to process and analyse these data. Movement data are complex, having a space and time dimension, and to do movement justice as a behavioural process requires sophisticated models. While this is met with a steady output of new methods for analysing the various components of movement

(e.g. Hooten *et al.*, 2017), including their implementations in the statistical software R (Joo *et al.*, 2019), we see three key directions in which advancement is required. First, tracking technology has improved to a point where we can observe movement paths at resolutions of multiple locations per minute, down to 1 Hz and lower (Weller-Weiser *et al.*, 2016). To go beyond descriptive analyses, or to avoid having to subsample data, we need to advance our inferential methods to handle high-resolution and highly autocorrelated data. Conceptually most promising is a switch to continuous-time movement models (Blackwell *et al.*, 2016). Applying these models is computationally more challenging than simpler methods based on discrete-time models, for example step-selection functions. However, implementation in statistical software will pave the way for more frequent application (Calabrese, Fleming, & Gurarie, 2016).

Second, when interested in communities, considering species interactions is imperative, including at the movement level. The majority of statistical methodology focuses on describing or inferring movement interactions between conspecifics. One branch of this addresses the question of leader–follower relationships or coherence in social groups, herds, or swarms (Calabrese *et al.*, 2018; Strandburg-Peshkin *et al.*, 2018). Another branch considers more generally movement behaviour in response to the conspecific population, revealing for example an overall conspecific attraction (e.g. Delgado *et al.*, 2014; Spiegel *et al.*, 2016). These methods may be transferrable to multi-species scenarios, however, most methods focus on one predominant behaviour within a group, population, or dyad (for a review of pairwise interaction indices, see Long & Nelson, 2013), not accounting for situations in which responses are highly individual specific or asymmetric (but see Schlägel *et al.*, 2019). Such flexible approaches, however, will be necessary to comprehensively assess interactions among heterospecifics in guilds or communities (e.g. Vanak *et al.*, 2013).

Third, it is increasingly the sheer amount of data that poses challenges to analysis. Data sets on movement become increasingly extensive in various dimensions. For example, tracking and biologging technologies yield ever more raw data points per individual, including multiple data streams per time stamp (e.g. spatial location, acceleration, temperature). Likewise, genetic sequencing methods (in particular, NGS) produce very large amounts of both raw sequence reads and processed decoded gene sequences. These ‘big data’ require sophisticated solutions not only to data archiving and sharing (e.g. standardized protocols for data collection and metadata management) but also to their analysis (López-López, 2016; Williams *et al.*, 2020). Analysis of high-frequency localization and biologging data may be rendered possible, for example, by distilling key movement characteristics (e.g. moves and turns; Potts *et al.*, 2018) before further statistical analysis. Population genomics can utilize available bioinformatics tools for sequence assembly and annotation. However, established and widely used open source software for subsequent population genetic dispersal inference has not always been adapted to handle genome-scale data sets

and is at times not capable of handling data sets comprising thousands of loci typed in thousands of individuals. Most promisingly, 'big data' are not unique to movement ecology, and thus analytical approaches will become available from other fields, for example human mobility research as well as data science and statistics more generally (Franke *et al.*, 2016; Thums *et al.*, 2018).

#### (4) Modelling emergent mobility and its consequences

Our ambition for a stronger integration of disciplines at the movement–community interface goes hand in hand with the need to cross levels of organization and scales along various axes. Here, computer-based simulation models, especially mechanistic, individual-based models (IBMs, also referred to as agent-based models), are a powerful tool because they allow us to let population-level features, such as growth rates, population structure, or spatial distribution, emerge from the adaptive behaviour of the individuals (Grimm & Railsback, 2005). Despite their great promise, IBMs of communities in which movement is based on first principles do not yet exist and will require integration of new data and experiments (see Sections V.1 and V.2). Mobility is still often represented *via* movement parameters that characterize fairly simple movement models such as correlated random walks, informed by observed turning angle and step-length distributions. Over the last two decades, however, the interaction of movement and habitat features is increasingly taken into account (Kramer-Schadt *et al.*, 2004), while explicitly linking movement decisions to established energy budget theories is a very recent development (Malishev, Bull, & Kearney, 2018). Here, IBMs might profit from mechanistic optimal annual routine modelling that determines the behavioural decision rules underlying movement based on energy and health budgets, taking evolutionary considerations into account (Schaefer *et al.*, 2018).

Presently, IBMs of communities are rarely linked to the theoretical concepts of modern coexistence theory, but they allow for measuring emerging population growth rates and determining niche differences. Here, a major obstacle to integrating the individual and population level lies in the different mindsets of researchers modelling from one or the other perspective. Coexistence theory is rooted in phenomenological population models, which lack a mechanistic description of the competition parameters. Carroll *et al.* (2011) suggested to define fitness and niche differences based on *per capita* growth rates from no-competition and invasion scenarios, which can be computed in simulation models (Chu & Adler, 2015). Recently, Ellner *et al.* (2018) proposed linking long-term growth rates to ecological processes *via* numerical simulations as a work-around of the typically only analytically considered mathematical equations of MCT. Similar approaches could be used to link outcomes of behavioural-based IBMs to community-level coexistence mechanisms. Another approach has been put forward by Jeltsch *et al.* (2019),

who suggest to extend the toolbox of population viability analysis, which often employs IBMs, to communities (termed coviability analysis). We advocate a further development and application of such approaches to make simulations more mechanistic in the sense that we look closer at how community-level patterns arise from movement processes through community-level mechanisms. In addition, we see merit in using IBMs to inform components or to test the assumptions of higher-level integration models. For example, we can use IBMs that include details about movement processes (and other behavioural mechanisms) to evaluate strongly summarizing mathematical formulations of population and community dynamics (Riotte-Lambert *et al.*, 2017). Or we can use IBMs to account for dispersal in hybrid species distribution models (Travis *et al.*, 2013; Singer *et al.*, 2016). In this way, one could, for example, also use models of genetic mobile-link movements to generate seed rains of animal-dispersed plants (Morales *et al.*, 2013).

As simulation models are increasingly being developed, they face challenges with respect to calibration, validation, and balancing complexity. IBMs typically have many parameters and complex structures, and some degree of freedom as to which parameter values and sub-model formulations to use. We can tie data into these decisions through pattern-oriented modelling (POM), in which various observed patterns are used as filters to reject unrealistic parameter combinations or submodels of specific key behaviours (Grimm & Railsback, 2012). Since patterns at the individual and higher levels are linked to each other, a lack of sufficient data at one level can be compensated by a set of distinctive patterns at the other level. In this way, we can use a set of community-level patterns (e.g. species richness, rank abundance, spatial distribution) to parameterize individual-level movement parameters. This can be performed in a statistically rigorous way through techniques like ABC, which uses likelihood-free sampling algorithms to generate posterior distributions for model parameters (Hartig *et al.*, 2011), and POM information criterion (Piou, Berger, & Grimm, 2009).

When many species are considered, it is key for IBMs to find generic representations of individuals of different species, and a generic representation of interactions between individuals, so that parameterization, runtime, and analysis remain manageable. To limit the number of different species to be considered, trait-based approaches have proven to be useful, where species are replaced by functional types that are characterized by certain trait combinations. These types can be imposed, based on observed trait combinations, or can emerge *via* community assembly from a pool of all possible trait combinations. Most existing realistic individual-based models of communities are forest or vegetation models, but a combination with animal functional types seems possible. Promising are allometric approaches to modelling movement distances, which can be applied across movement types and movement

modes (Viana *et al.*, 2016; Hirt *et al.*, 2018; Teckentrup *et al.*, 2018).

### (5) Communities under environmental change

As demonstrated above, movement processes are an integral part of community assembly and several key coexistence mechanisms. As a result, community composition is expected to respond to altered movements in the wake of an increasing human footprint on the environment (Harris *et al.*, 2009; Tucker *et al.*, 2018). Climate change and human land use are among the main global environmental change drivers (Tylianakis *et al.*, 2008). At an individual level, they modify how, when and where organisms move, as movement processes across taxa and scales are tightly linked to the environmental conditions that organisms experience.

Climate change can affect any component of the movement process. In the most direct way, climate warming influences motion capacity *via* the thermal sensitivity of physiological processes involved in locomotion (Gibert *et al.*, 2016). Indirectly, climate change affects dispersal capacities of organisms that disperse *via* abiotic vectors such as water and wind, for example by modifying ocean circulation patterns with significant effects for many marine taxa (Wilson *et al.*, 2016). Also at smaller scales, regional changes in wind speed impact the transport of plant propagules, affecting both average dispersal distances and the chance of long-distance dispersal events (Bullock *et al.*, 2012). Dispersal behaviour is further expected to change due to evolutionary pressures under climate change (Travis *et al.*, 2013). Climatic conditions also contribute to the environmental cues that drive migration. Over recent decades, migratory patterns of many species have been observed to change, involving shifts in timing, reduced extent of migrations, or increased proportions of sedentary individuals in partial migrants, with climate change likely being a key driver (Seebacher & Post, 2015). Some migratory animals may even switch their movement type, becoming nomadic in response to reduced predictability of environmental conditions (Harris *et al.*, 2009).

With increasing anthropogenic land use, biodiversity has become seriously threatened by habitat loss and degradation, often accompanied by fragmentation. At the landscape scale, fragmentation may hinder dispersal by increasing the distances required to reach new habitat patches and posing challenges to the transience phase. For example, orientation in an agricultural matrix can be hampered, especially for non-flying animals such as small reptiles in tall crops (Kay *et al.*, 2016), and sublethal doses of insecticides can negatively affect insects' cognitive abilities, including their memory and navigation capacities (Tison *et al.*, 2016). In addition, strong habitat specialists may perceive matrix (i.e. landcover between habitat patches not providing for self-sustaining populations) as a barrier and move greater distances to take detours (Knowlton & Graham, 2010). Yet this cannot be generalized and requires consideration of species' mobility (Kniowski & Gehrt, 2014) or internal state (Keeley *et al.*,

2017). Another obstacle to movements are roads and railways, and their effect on mobility depends on movement-related factors such as familiarity with passage locations (Ascensão *et al.*, 2014). At the other extreme, the removal of historical dispersal barriers through human trade and transport activities is problematic with respect to invasive species and disease spread (Hulme, 2009). Non-human biotic vectors, that is genetic linkers, may likewise act as primary introducers (Reynolds *et al.*, 2015), but also play a critical role in secondary dispersal once introduced (Moravcová *et al.*, 2015).

With a heightened awareness of the importance of movement for other ecological processes and higher-level patterns (Jeltsch *et al.*, 2013; Bauer & Hoyer, 2014; Barton *et al.*, 2015; Jönsson *et al.*, 2016), more research is now focused on the links between environmental change, movement processes, population and species persistence, and community dynamics. However, few studies connect all of these components. Therefore, we need a framework that joins the different parts of the story, and we hope to contribute to this with our framework of movement-mediated community assembly and coexistence.

## VI. CONCLUSIONS

(1) Any component of individual-level movement processes, as summarized in the movement ecology framework, can scale up to significant effects for metacommunity dynamics, community assembly and species coexistence. Although they work in unison, often one or two case-specific components may be critical in their effect at the community level. Identifying these key components in individual systems will improve our understanding and prediction of (meta-)community structures and biodiversity patterns.

(2) Despite an increasing awareness of the importance of movement for other ecological processes, there remains a gap between studies that investigate the details of movement, which are typically single-species studies, and studies that examine community composition, in which movement is often considered simplistically at the species level. This gap is likely due to large differences in timescales between individual movement processes and community-level effects and is also reflected in an imbalance in data availability and analysis of movement types. While dispersal is typically considered from the community perspective and data on the transience stage are underrepresented, data on station-keeping movements are widely investigated at the process level but are rarely scaled up to community level. Migration and nomadism are often considered with a population perspective; a stronger community perspective with respect to direct effects of movement is still lacking while the potential for mobile link effects has been tapped.

(3) To achieve a true integration of individual-based and community-based perspectives and bridge the identified gaps, we need concepts that link both perspectives and bring

together new observations, experiments, and computational tools:

(i) We must recognize the emergence of species' mobility and mobile-link generated patterns from individual-level movement processes, including feedbacks between processes and patterns.

(ii) We recommend to make use of improved data availability thanks to direct and indirect tracking methods to extend movement-process studies to small taxa and to track multiple individuals of different species of ecological communities concurrently.

(iii) Facilitated by tracking technology, experiments can be set up with the same design both in the laboratory with microorganisms and in the field with macroorganisms to test causal links between movement mechanisms and community-level patterns and thereby complement observational studies.

(iv) We urge for an advancement of statistical methods to keep up with the analyses of newly available rich data sets. In particular, we must learn to handle 'big data', to fully utilize multi-species, high-resolution tracking data, and to optimally integrate direct (e.g. from tracking) and indirect (e.g. from gene sequencing) movement data.

(v) We expect computer-simulation models to increase in their applicability in extrapolating insights from short-timescale observations and experiments to ecological timescales through complexity-reducing trait-based approaches and improved parameterization from data, facilitated by advances in movement data collection. We expect simulation models to become a major tool in identifying key components of movement processes for specific systems and community-level processes and to generate appropriate aggregative formulations of movement in higher-level integration models.

(4) In addition to increasing awareness of the many ways in which movement processes affect the mechanisms that drive community composition, we hope to achieve two main goals: to encourage community ecologists to consider more explicitly the complexities of movement processes and to stimulate movement ecologists to perform more multi-species analyses within and across trophic levels and to link these to community-level mechanisms.

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